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AESTIVATION OF COCONUT FLOWERS

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The flowers of the coconut, male as well as female, have six perianth lobes each. This report essentially deals with the arrangement of the perianth segments in the flowers.

The three outer perianth segments correspond to the sepals, and the inner three, the petals. In a male flower of coconut, the sepals are always imbricately arranged. That is, one sepal remains completely outside the other two, having both its wings exposed. The innermost sepal has its wings overlapped by the other two sepals on either side. The middle sepal has one of its wings overlapped by the outermost sepal, and the other exposed. Depending on the position of the exposed portion of the middle sepal, a flower may be regarded as leaf-handed or right-handed. The left-imbricating and right-imbricating male flowers in any coconut palm are distributed more or less in a 50 : 50 proportion. Similar data on six other palm species are also presented.

The three petals in the male flowers of coconut are valvate, and so they do not manifest any overlapping.

In the female flowers, there are six large perianth segments which completely cover the ovary until the stage of receptivity. The three sepals are always imbricate like those of the male flowers. But the three petals either regularly twist (contort), or imbricate like the sepals. In any large population, about ten per cent of the female flowers will have contorted corolla. Corresponding figures were worked out for seven other species of palms, and the percentages ranged from zero for *Ptychosperma macarthurii* to 33.2 for *Phoenix paludosa*.

The calyx-corolla relationship on their aestivation was studied from another set of coconut fruits. There is a positive association of fruits having one type of sepal-arrangement with those having the opposite type of petal-aestivation. This characteristic becomes much more clear in *Ptychosperma macarthurii*.

The arrangement of the perianth of a coconut fruit has no association with either the foliar spiral of its mother palm, or that of the seedling that germinates from the fruit.

INTRODUCTION

The flowers of palms, especially the males, are very small, and their perianths are still smaller. That is why perhaps the study of the perianth aestivation in palms has not received any appreciable attention.

As the size and form of trunks, leaves, inflorescences and fruits of palms show great variation between species and even between individuals of the same species, their flowers also exhibit amazing diversity in form, structure as well as distribution on the peduncle. The flowers of palms are borne on fairly stout semi-fleshy spikes which are covered when young by one or more spathes, thereby the palm inflorescence getting the name, spadix. Though the flowers of a few species such as *Washingtonia robusta* are hermaphrodite, those of a great majority of species are unisexual : pistillate and staminate. Both these kinds of flowers may be produced on the same tree (monoecious) as in *cocos nucifera, Areca catechu* and several others, or in different individuals (dioecious) as in *Borassus flabellifer, Phoenix sp.* etc. Some species are polygamous since they bear perfect flowers as well as male and/or female flowers. In some species of *Phytelephas, Nypa, Elaeis* and a few others, the female flowers cluster in separate dense spadices and the males are distributed on different slender spadices in the same palm. However, in many other monoecious palms, the male and female flowers are generally distributed throughout the rachises (spikes) although in species like *Cocos nucifera* and *Areca catechu*, the female flowers occupy the

lower positions, the distal region being entirely occupied by the males. The frequent arrangement in the rest of the monoecious palms is a cluster of two male flowers with a female in between them.

Most palm flowers are sessile and are partially buried in the rachis, but some, such as the female flowers of *Corypha elata* or *Hyphaene indica* have short pedicels. A perfect flower has usually two whorls of 3+3 perianth lobes, a whorl of stamens ranging from 3 toα, and a whorl of carpels numbering usually three. The carpels may be united, or fully or partially free. The outermost whorl of three perianth lobes represents the calyx, and the inner whorl corresponds to the corolla in dicotyledonous flowers.

PERIANTH OF MALE FLOWERS

The arrangement of perianth lobes in palm flowers is variable. But it is customary to mention their aestivation as imbricate (Hooker, 1894 ; Blatter, 1926 ; Patel, 1938 ; Raghavan and Baruah, 1956 ; Menon and Pandalai, 1958 ; Nixon, 1959 ; Murthy and Bavappa, 1960 ; Bruce Ledin, 1961 ; Lawrence, 1963 ; Child, 1964 ; Fremond *et al*, 1966). To mention an example, Lawrence describes thus, ' perianths of 6 segments (vestigial in *Phytelephas*), in 2 series, free or connate, sepals generally imbricate or open in bud, petals mostly valvate in staminate flowers and imbricate in the pistillate.'

On critical examination of numerous flowers of a few species of palms, it was found that the aestivation of the perianth segments is not so simple as to be described as either valvate or imbricate. Over ten thousand female and several male flowers of the coconut and the following eight other species of palms were examined for the arrangement of their perianths ; *Areca catechu*, *A. triandra*, *Borassus flabellifer*, *Caryota mitis*, *C. urens*, *Phoenix paludosa*, *P. sylvestris* and *Ptychosperma macarthurii*. The flowers/fruits, collected mostly from palms growing within the premises of the Indian Statistical Institute, Calcutta were examined during different seasons between 1964 and 1967. In addition, several fruits, of *Chrysalidocarpus lutescens*, *Hyphaene indica*, *H. thebaica*, *livistona chinensis* and L. *rotundifolia*, where the perianths are either very small and valvate or vestigial, were also examined. The male flowers of all the species examined possessed only valvate petals. But the sepals in most of them were imbricate. The male flowers of *Borassus flabellifer* possess valvate sepals and tubular corolla having valvate lobes. Even with a dissecting microscope it is often difficult and time consuming to study the aestivation of the male flowers in some species.

Table I shows the data on the aestivation of sepals of male flowers of seven species.

TABLE I

Palm flowers : Aestivation of sepals of male flowers

Species	CL	CR	IL	IR	Total
Areca catechu	—	—	12	18	30
Arenga pinnata	1	5	170	168	344
Caryota mitis	—	—	716	711	1427
Caryota urens	—	—	174	104	278
Cocos nucifera	—	—	110	145	255
Phoenix sylvestris	—	—	48	51	99
Ptychosperma macarthurii ...	—	—	101	104	205
Total ...	1	5	1331	1301	2638

CL = left-contortion : CR = right-contortion.
IL = left-imbrication : IR = right-imbrication.

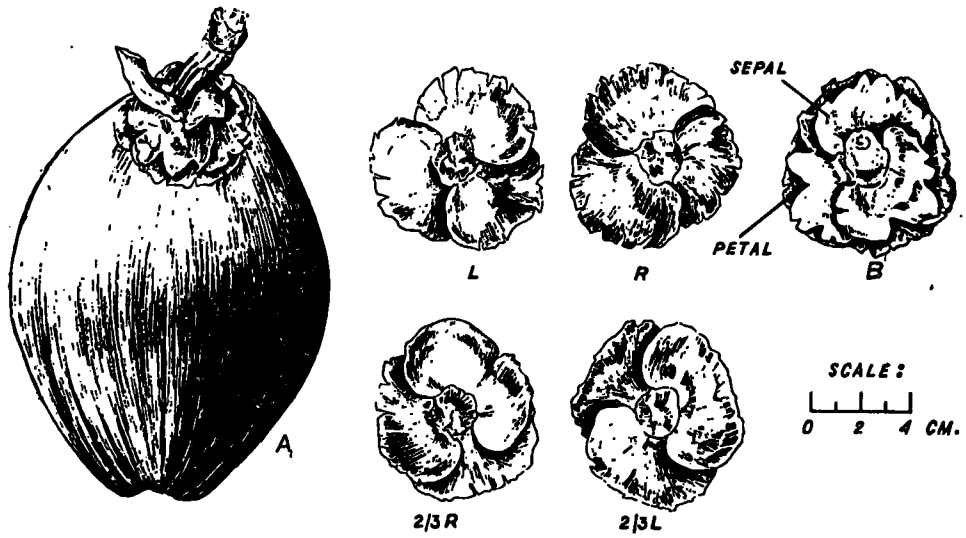

FIGURE 1. A — a coconut fruit with perianth.
B — sepals and petals as they appear on a fruit ;
L, R — petals regularly twisting to the left and right respectively ; 2/3 R, 2/3 L—petals imbricating to the right and left respectively.

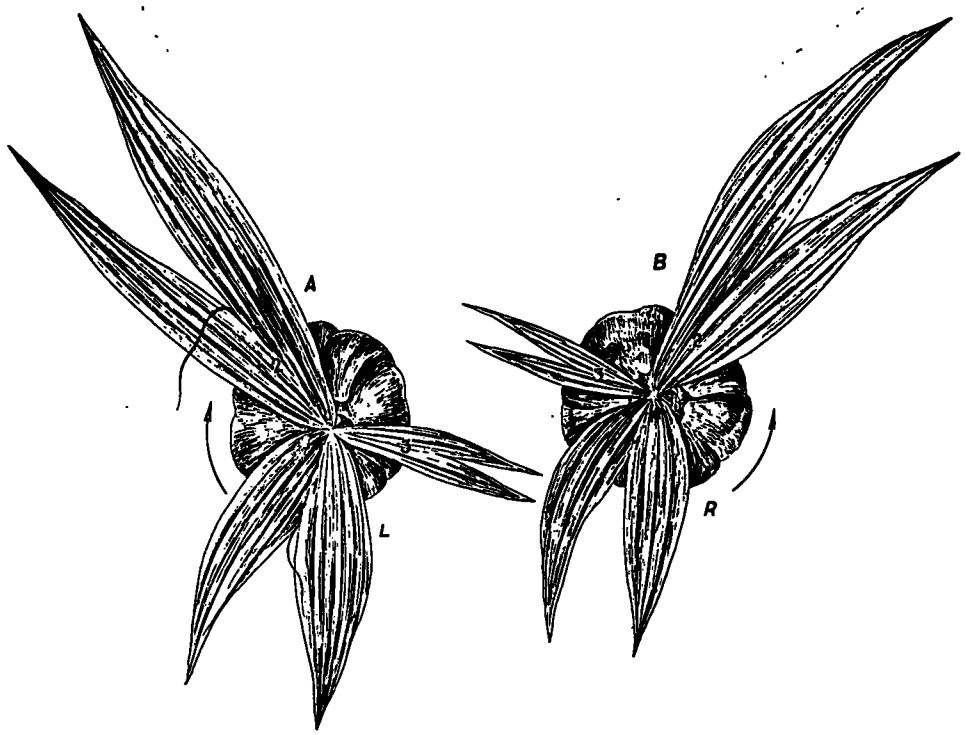

FIGURE 2. Seedling A will eventually develop right-handed foliar spirals, and B left-handed foliar spirals when the directions of the five spirals are considered. In A, the consecutive leaves are arranged clockwise (Left), and in B, counterclockwise (Right).

Only in *Arenga pinnata*, six of the 344 flowers had contorted calyx. Although the consolidated figures show that the left- and right-handed flowers are distributed more or less in a 1 : 1 ratio, the left-handed flowers are significantly more than the right-handed ones in *Caryota urens*.

THE FEMALE FLOWERS

The female flowers of many species of palms are much larger than the males, and the perianths fully cover the ovary up to the stage of receptivity. Determination of the aestivation of perianths of female flowers is thus relatively easy.

The outer whorl of perianths of a female flower representing the sepals is invariably imbricate in most species. In such an arrangement, the outermost sepal remains fully exposed and the innermost one is overlapped on both the sides by the other two sepals. One half of the middle sepal is overlapped by the outer sepal and the other half, which is exposed, overlaps a portion of the innermost sepal. In very exceptional cases, the sepals are regularly twisted (contorted) as in *Borassus flabellifer*. The inner whorl of three perianth segments corresponding to the corolla either imbricates or regularly contorts. In *Caryota mitis*, *C. urens*, and a few others, the petals of female flowers are valvate, but their sepals are imbricate, a condition similar to their male flowers.

Where all the petals contort, the direction of rotation may be either clockwise or counter-clockwise (Fig. 1, L & R). The number of flowers/fruits having clockwise contortion approximately equals those having counter-clockwise contortion in any species. Also among the flowers having imbricate corolla, two kinds are noticed. If the left half of the middle petal of an imbricating flower is exposed, the flower is regarded as imbricate-left-handed (2/3 left-handed), and imbricate-right-handed (2/3 right-handed), if the right half is exposed, (Fig. 1, 2/3, L & 2/3 R). In each of the species, the flowers having left-handed and right-handed contortion occur almost equally ; so also those with left-handed and right-handed petal-imbrications occur almost in equal proportions.

The ratio of flowers having contorted corolla to those with imbricate corolla varies very greatly with species. To estimate the degree of the variation, data were collected on numerous flowers/fruits of eight species and these are presented in Table 2.

TABLE 2

Aestivation of petals of female flowers/fruits in 7 palm species.

Species	Corolla contorted		Corolla imbricate		Total
	Left	Right	IL	IR	
Areca catechu	320	275	1225	1219	3039
Areca triandra	9	6	182	206	403
Borassus flabellifer	25	38	143	143	349
Cocos nucifera	32	34	316	304	686
Phoenix dactylifera	5	3	36	30	74
Phoenix paludosa	42	19	62	61	184
Phoenix sylvestris	384	253	1083	961	2681
Ptychosperma macarthurii ...	0	1	1195	1128	2324
All species	817	629	4242	4052	9740

The percentage of contorted flowers in a population sampled for *Areca triandra* was only 3.7, that for *Cocos nucifera* 9.6, *Phoenix dactylifera* 10.8, *Borassus flabellifer* 18.1, *Areca catechu* 19.6, *Phoenix sylvestris* 23.8 and *Phoenix paludosa* 33.2. In the case of *Ptychosperma macarthurii*, however, with the exception of a single flower, a population of 2324 flowers showed only imbricate corolla.

It is obvious from the data in Table 2 that the sum of flowers/fruits having left-contortion and left-handed imbrication is greater than that of their counterparts. The mechanism which regulates the aestivation of the corolla is not yet known. As the number of foliar spirals varies with species (as for example, *Borassus flabellifer* has *3 spirals*, *Cocos nucifera 5*, *Phoenix sylvestris* 8 and so on), perhaps the foliar arrangement has some bearing on the aestivation.

CALYX-COROLLA RELATIONSHIP IN COCONUT

In the male flowers of coconut, the calyx is always imbricate and the corolla valvate. In about 50 per cent of the male flowers, the sepals imbricate to the left and in the rest they imbricate to the right.

Among the female flowers, the sepals in a flower either imbricate to the left or to the right, and the two kinds of flowers occur almost equally. As per data shown in Table 2, the corolla either twists regularly or imbricates. Therefore, it was decided to examine the relationship in the arrangements of the sepals to the petals. The sepals and petals of 734 fruits were critically examined by removing them one after another and recording their arrangement. The data are presented in Table 3.

TABLE 3

Cocos nucifera : Calyx-corolla relationship.

Sepals	*Petals*				*Total*
	Contortion		*Imbrication*		
	Left	*Right*	*Left*	*Right*	
Left contortion	—	—	—	—	—
Right contortion	—	—	—	—	—
Left imbrication	8	35	175	196	414
Right imbrication	32	8	149	131	320
Total ...	40	43	324	327	734

Among the 734 fruits examined, none had regularly twisting (contorting) calyx. 11.3 per cent of the fruits had contorting corolla. The corresponding figure for *Cocos nucifera* reported under Table 2 is slightly less (9.6 per cent). This variation may be expected between samples collected during different seasons. If the figures in Table 3 are examined critically, it will be seen that among the fruits having contorting corolla, there is a great association of left-imbrication of sepals with right-contortion of petals, and *vice versa*. Similarly, among the fruits having

imbricate corolla, there is a small preference for a fruit with a particular sepal-imbrication to associate more with the opposite type of corolla-imbrication. This peculiarity is vividly revealed in the data on *Ptychosperma macarthurii* where all the fruits have only imbricating corolla. The data are presented in Table 4.

TABLE 4

Ptychosperma macarthurii : Calyx-corolla relationship

Sepals	*Petals*				*Total*
	Contortion		*Imbrication*		
	Left	*Right*	*Left*	*Right*	
Left contortion	—	—	—	—	—
Right contortion	—	—	—	—	—
Left imbrication	—	—	21	309	330
Right imbrication	—	—	292	7	299
Total ...	—	—	313	316	629

The significance of the preponderant preference for a fruit to have its sepals and petals veering oppositely is not clear. Though this preference is clearly demonstrated in *Ptychosperma macarthurii* and less so in *Cocos nucifera*, there are species like *Areca catechu* and *Borassus flabellifer* where the sepal-petal arrangement does not show any preference for any particular combination.

AESTIVATION OF PERIANTH AND FOLIAR SPIRAL OF SUBSEQUENT SEEDLINGS

No correlation has been found to exist between the foliar spiral of a coconut palm and the aestivation of the perianth lobes of its fruits. Both the left-spiralled and right-spiralled palms produce approximately equal numbers of fruits with left-handed and right-handed aestivation.

In order to find out whether there is any association between the spirality of the corolla of a fruit and the foliar spiral of the seedling that germinates from it, a small number of seed-nuts were collected from 12 young palms at the Indian Statistical Institute, and their aestivation recorded. The nuts were sown in a special nursery and the seedlings (when having only two laminate leaves each) were examined and the direction of the foliar spiral recorded.

Fig. 2 shows a right-spiralled and another left-spiralled coconut seedling.

To avoid a possible confusion in the determination of foliar spiral in young coconut seedlings, the procedure is explained briefly. The leaves of the coconut palm are alternate and arranged

one after another. Two consecutive leaves make an angle of about 138° between them. According to Sampson (1923), this angle is 142°. But Patel (1938), working on a great number of coco nut palms belonging to different age groups, reported that each new leaf is set at an angle varying from 137° to 141° from the previous one. An observer facing the base of a particular leaf may find the next younger leaf nearer either to his left hand side or to the right. If the younger leaf is nearer to the observer's left, the foliar spiral of the palm will be regarded right-handed, and *vice versa* if the younger leaf is to the observer's right. This can be explained further. The phyllotaxy of coconut spiral is nearly two-fifths. That is, the sixth leaf comes almost above the first one. The sum of the five angles (between six leaves) makes 700° (assuming the angle between two consecutive leaves to be 140°) which falls short of two complete revolutions by 20°. Therefore, in a palm where the second leaf is nearer to the first on the left side, the sixth leaf will remain on the right side of the first leaf by 20°. Also, leaf number 11 will fall 20° to the right of leaf number 6 (or 40° to leaf number one). The leaves 1, 6, 11, 16, 21, 26 . . . form one of the five spirals on the coconut crown. The other four spirals also run along the same direction (right) as the first spiral. Thus, in a palm where the second leaf is nearer to its immediate older leaf by the right, the five foliar spirals will be veering clockwisely (left-handed). There are a few other ways of determining the foliar spiral of the coconut which have been already explained (Davis, 1962). The direction of the foliar spiral in *Cocos nucifera* is not determined genetically. Though the left-hand right-spiralled palms are distributed more or less equally in a region, there is a difference in the proportions of the lefts and rights between the two hemispheres (Davis, 1964).

Table 5 gives data on the foliar spiral of 138 seedlings. The perianth patterns of the fruits giving rise to these seedlings were known.

TABLE 5

Cocos nucifera : **Aestivation of fruits and spirality of subsequent seedlings**

Aestivation of fruit : *Sepals* : *Petals*		*Foliar spiral of seedlings* *Lefts*	*Rights*	*Total*
Imbricate Left	Contorted Left ...	—	—	—
	Contorted Right ...	3	4	7
	Imbricate Left ...	23	9	32
	Imbricate Right ...	15	19	34
Imbricate Right	Contorted Left ...	—	3	3
	Contorted Right ...	—	1	1
	Imbricate Left ...	14	11	25
	Imbricate Right ...	24	12	36
Total		79	59	138

Note.—One fruit with 2 sepals and 2 petals produced a seedling having left foliar spiral ;
Two fruits each with two sepals and petals imbricating to the left produced seedlings one having left spiral and other right spiral.

It is clear from the data given in Table 5, that the foliar spiral of a seedling does not depend on the aestivation of the fruit. This is also expected since the perianth is a maternal organ, while the seedling (embryo) is the product of the mother and invariably a different unknown pollen parent, as cross fertilization is the general rule in the coconut, especially the Tall variety.

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